

**MESOPHYLETIS CALHOUNI (MESOPHYLETINAE), A NEW GENUS, SPECIES,
AND SUBFAMILY OF EARLY CRETACEOUS WEEVILS (COLEOPTERA:
CURCULIONOIDEA: ECCOPTARTHRIIDAE) IN BURMESE AMBER**

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Abstract.—A new subfamily, genus and species of weevils (Coleoptera: Curculionoidea; Eccoptarthridae: **Mesophyletinae: *Mesophyletis calhouni* Poinar**) are described from Cretaceous Burmese amber. This fossil differs from all previously described Cretaceous weevils in having definite geniculate antennae with an elongate scape and antennal scrobes, prolonged trochanters, toothed tarsal claws, and long pedunculate lobes on the third tarsal segment. The presence of the latter characters suggests that its life style was arboreal.

Key Words: Eccoptarthridae, Mesophyletinae, new subfamily, *Mesophyletis*, new genus, *Mesophyletis calhouni*, new species, Burmese amber, Early Cretaceous, Curculionoidea

Mesozoic weevils are uncommon and almost all belong to the primitive weevil Division Orthoceri, which include species with straight antennae (Alonso-Zarazaga and Lyal 1999; Gratshev and Zherikhin 2003; Ponomarenko 1995; Zimmerman 1993, 1994a). Thus it was of interest when a weevil in Early Cretaceous Burmese amber was discovered with definite geniculate antennae. The present study describes this weevil and discusses its possible biological affiliations based on functional morphology.

MATERIALS AND METHODS

The amber piece containing the fossil is roughly square in outline, measuring 8 mm long by 7 mm wide and 3 mm in depth. Observations, drawings, and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 600 \times .

Amber from Burma occurs in lignitic seams in sandstone-limestone deposits in the Hukawng Valley. Nuclear magnetic resonance (NMR) spectra of amber samples taken from the same locality as the fossil indicates an araucarian (possibly *Agathis*) source of the amber (Lambert and Wu, unpublished research 2002). Palynomorphs obtained from the amber beds where the fossil piece originated have been assigned to the Upper Albian of the Early Cretaceous (100–110 mya) (Cruikshank and Ko 2003).

The Burmese amber weevil is well preserved and complete, with all its appendages still attached (Fig. 1). Since it could not be placed in any extant or extinct genus, it is described below in a new subfamily of the family Eccoptarthridae. Systematic treatment of families and subfamilies is based, in part, on that of Alonso-Zarazaga and Lyal (1999).

Superfamily Curculionoidea Latreille
Family Eccoptarthridae Arnoldi 1977

Diagnosis.—Small to medium-sized weevils (under 10 mm); rostrum medium to long, usually slender, nearly straight to slightly curved; antennae straight or elbowed (geniculate), normally attached near middle of rostrum; club loose or somewhat compact; eyes round, small to large, often positioned closer to upper surface of head; pronotum transverse, almost flat to curved; legs mostly short; forecoxa large, often situated close to hind margin of prothorax; femora thickened, unarmed; tibia straight, often emarginate; tarsi variable, tarsus 1 often widened, tarsus 3 distinctly bilobed; claws simple or divided; elytra broad or elongate, nearly flat to slightly concave, with irregular or regular rows of fine punctures; wings present; scutellum present or absent; abdomen with at least segments 2–4 subequal.

Comments.—The diagnosis provided here is based on characters common to the genera listed by Alonso-Zarazaga and Lyal (1999) in the subfamilies Eccoptarthrinae Arnoldi and Baissorhynchinae Zherikhin. I follow Zimmerman (1994a) in establishing family status for the carids, thus removing the Carinae from the Eccoptarthridae. Thus, the Eccoptarthridae consists only of fossil genera. The characters presented under the family diagnosis are general because they are usually the only ones observable in fossils, especially compression fossils. Many crucial characters (genitalia, mouthparts, structure of antennal club, etc.) are not included because they are rarely preserved, or if they are preserved, are obscured.

Mesophyletinae Poinar, new subfamily

Description.—Antenna geniculate with elongate scape and scrobes; antennal funiculus 6–7 segmented; antennal club loosely 3 segmented; eyes large, round;

pronotum transverse; trochanters enlarged or prolonged; tarsal claws paired, widely divergent, simple, bifid or appendiculate; abdominal ventrites with straight sutures; elytral tips obtuse, pygidium exposed.

Diagnosis.—The diagnostic characters of this fossil subfamily are geniculate antennae, enlarged or prolonged trochanters, and exposed pygidium. The genus *Cretonanophyes* Zherikhin is transferred from the Eccoptarthrinae to the Mesophyletinae because it contains the above mentioned diagnostic characters.

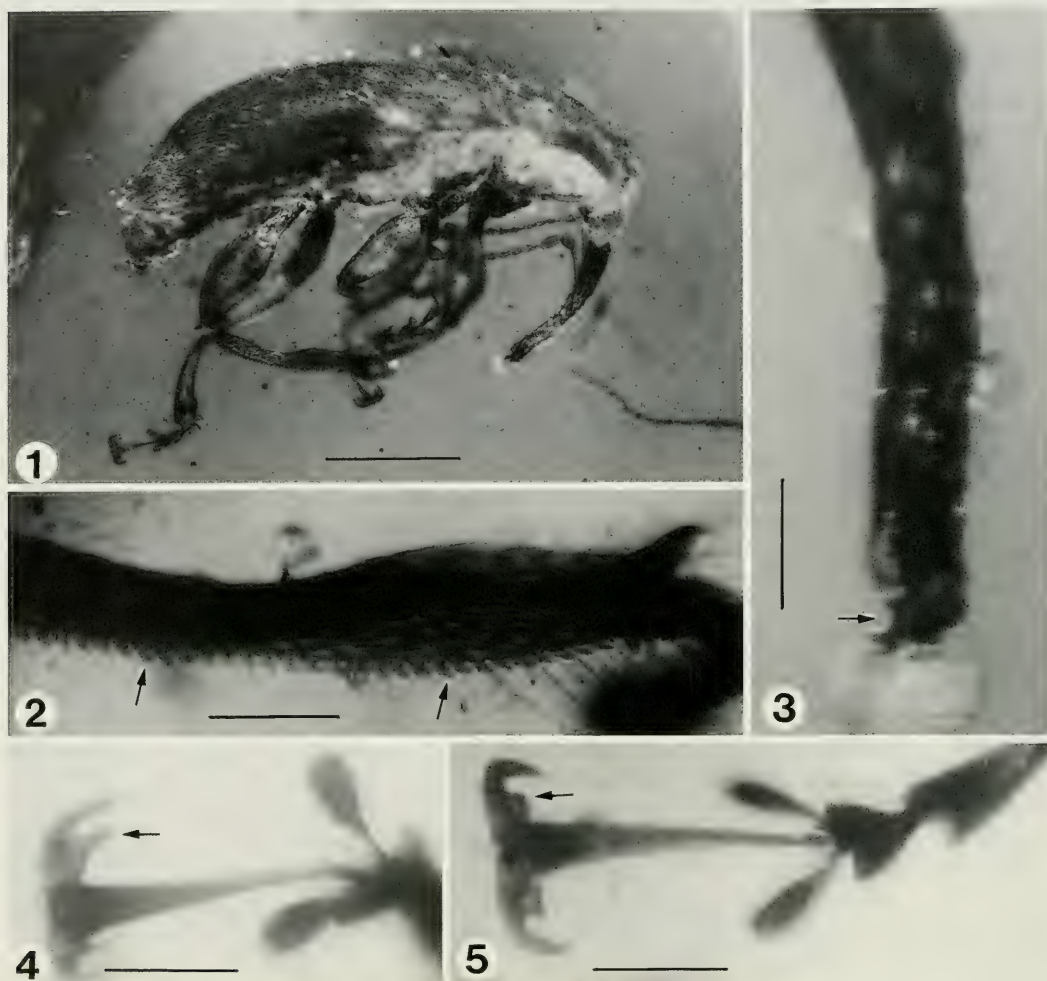
Comment.—A drawing of the Late Cretaceous *Cretoacar luzzi* Gratshev and Zherikhin (2000) shows one antenna straight and the other elbowed; however, no mention is made in the description as to whether the antennae are geniculate or not and the ratio of scape/funicle is 0.36, which is low for geniculate antennae. An examination of select extinct and extant weevil species of various taxa by the author showed that the great majority with geniculate antennae have a scape/funicle ratio greater than 0.50. Both *Mesophyletis* and *Cretonanophyes* have a scape/funicle ratio greater than 0.50.

***Mesophyletis* Poinar, new genus**

Type species: *Mesophyletis calhouni* Poinar.

Description.—With characters listed under subfamily description; eyes positioned on dorsolateral side of head; antennal insertions on side of and approximately in middle of rostrum; antennal scape long, reaching anterior border of eye; scape/funicle ratio, 0.82; antennal scrobes exposed in side view; pronotum transverse; forecoxa large, close to hind margin of prothorax; tarsal claws toothed.

Diagnosis.—*Mesophyletis* differs from all previously described Mesozoic weevils in having pedunculate lobes of the third tarsal segments and bifid claws. Also, its geniculate antennae with an elongate



Figs. 1–5. *Mesophyletis calhouni* in Burmese amber. 1, Lateral view (right side) of holotype female. Bar = 691 μ m. 2, Lateral view of metatibia showing serrations (arrows). Bar = 127 μ m. 3, Lower portion of rostrum showing exodont mandible (arrow). Bar = 98 μ m. 4, Pedunculate lateral lobes and elongate terminal mesotarsal segment with pointed inner (arrow) and outer teeth of bifid claws. Bar = 100 μ m. 5, Terminal metatarsal segment with blunt inner (arrow) and pointed outer teeth of claws (arrow). Bar = 100 μ m.

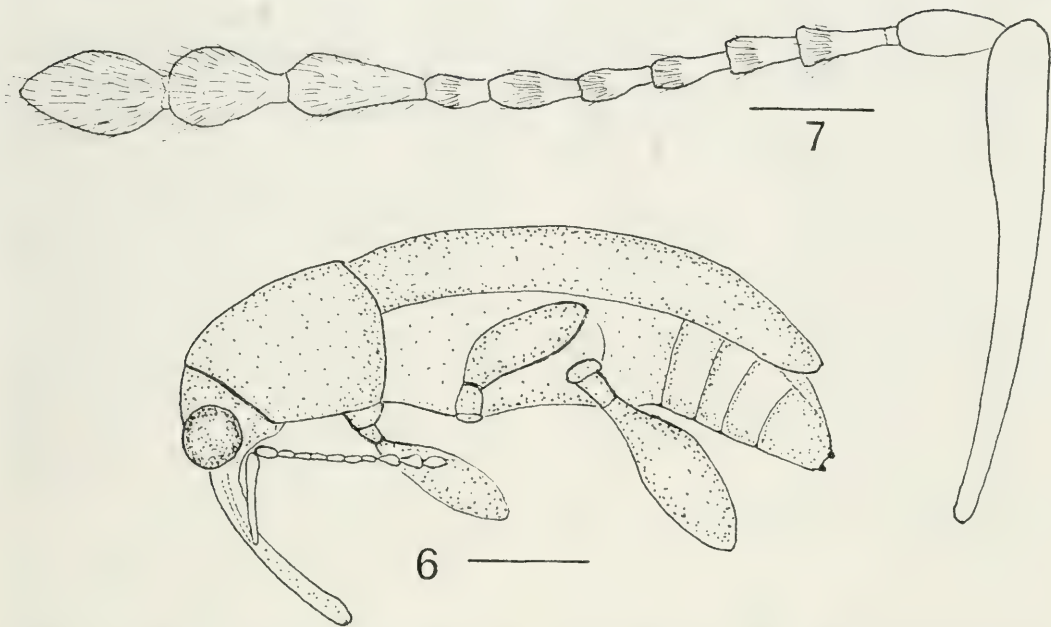
scape and antennal scrobes separate it from all Mesozoic weevils except *Cretonanophyes longirostris* Zherikhin. *Cretonanophyes* differs from *Mesophyletis* in its longer rostrum, width of its ventrites, position of the pro- and mesocoxae, and its simple claws.

Etymology.—*Mesophyletis* is from the Greek “meso” for something between and the Greek “phyle” for tribe or race. The gender is feminine.

***Mesophyletis calhouni* Poinar, new species**
(Figs. 1–7)

Description.—Female; characters as listed under family and generic diagnoses. Body length 2.8 mm.

Head: Head deflexed, 1.3 mm long; eyes round, protruding from head margin; located at base of rostrum; rostrum long, slender, curved more at base than apex; antennal scape 419 μ m long, swollen at apex; antennal funiculus composed of 7



Figs. 6-7. *Mesophyletis calhouni* in Burmese amber. 6, Lateral view (left side) of holotype female. Note geniculate antenna and prolonged trochanters. Bar = 505 μm . 7, Detail of antenna. Note long scape and loose club. Bar = 95 μm .

segments, length of funicular segments: 1: 95 μm , 2: 89 μm , 3: 63 μm , 4: 68 μm , 5: 63 μm , 6: 79 μm , 7: 53 μm ; club composed of three loosely joined segments, length of club segments: 1: 116 μm , 2: 105 μm , 3: 131 μm ; first and second funicular segments subequal in length; funicular segments with hair bands; club segments uniformly covered with dense hairs; ratio of scape/funicle, 0.82; exodont mandibles positioned vertically; maxillary and labial palps not observed.

Thorax: Brown, pronotum 890 μm long, transverse; densely pubescent; with rounded edges; lacking lateral carina; procoxa prominent, separated by a keel-like prosternum; mesocoxae closely approximate; metacoxae well separated; trochanters prolonged; femora clavate, somewhat flattened, unarmed; meso- and metafemora curved; tibiae strongly flattened; pro- and mesotibiae bearing well-developed spine at apex; metatibia serrulate with 2 broad symmetrical spines at apex; smaller denticles on mesotibia;

denticles absent on protibia; tarsi 5-segmented, first tarsal segment straight to slightly notched; second tarsal segment explanate and notched at tip; third tarsal segment greatly bifid with pedunculate lateral lobes; fourth tarsal segment miniscule, located at base of fifth segment; fifth tarsal segment greatly elongate, narrow at base, tarsal claws widely divergent, bifid (on pro- and mesotarsi) or appendiculate (laminar) (on metatarsi); elytra bicolored, with prominent shoulders; elytral vestiture fairly dense; anterior third and posterior sixth with castaneous colored squamae, remainder black except for elliptical castaneous spot in anterior mid-portion of black area; elytra tapered posteriorly, with prominent suture extending total length; each elytron with approximately 25 rows of depressed setae; elytral apices bluntly rounded, exposing pygidium; elytral striae not visible; elytral surface, especially apical half, covered with minute protuberances; scutellum not visible.

Abdomen: Dark brown; 2.2 mm long; five ventrites present, all leveled; 2–4 subequal in width; tip of abdomen rounded, with two small protruding appendages considered to be styli of the hemisternites; pygidium exposed.

Male unknown.

Material examined.—Holotype female in Burmese amber from the Hukawng Valley, deposited in the Ron Buckley amber collection located at 9635 Sumter Ridge, Florence, KY, 41042. This collection is available to scientists for study, and plans are underway to transfer it to a major museum.

Etymology.—The specific epithet “calhouni” is for the memory of John Calhoun.

Comment.—It is unusual for the shape of the claws to differ on the same individual. While on the pro and mesotarsi both the inner and outer teeth are pointed (bifid), on the metatarsi the inner tooth is blunt tipped (appendiculate) and the outer one is pointed (Figs. 4, 5). This difference of claw types is not due to the viewing angle. The other interesting and apparently unique feature for at least fossil weevils is the pedunculate lobes of the third tarsal segments.

DISCUSSION

In his treatise on Australian weevils, Zimmerman (1993; 1994a, b) divided the Superfamily Curculionoidea into three Divisions. The Orthoceri included the primitive weevils with straight antennae, the Gonatoceri contained the advanced weevils with geniculate antennae, and the Heteromorphi consisted of those species that did not clearly belong to either of the above but showed some features of each. In this classification, *Mesophyletis* would fall into the Division Heteromorphi.

The shift from a short to a long scape in weevils is an evolutionary trend that also occurs in the Hymenoptera, especially in social forms like ants where the more

primitive forms possess a short scape and the advanced ants a longer one. Benefits of a longer scape in ants are considered to be improved cardanic movements between the scape and funicle, thus enabling better inspection of the brood and recognition of food items (Baroni Urbani 1989). While brood care cannot be considered the selective force for a long scape in weevils, being able to extend the antennal clubs for better inspection of plant surfaces for feeding and oviposition and detecting sensory signals from plant hosts could be important factors, especially in the Cretaceous when the angiosperms were evolving and forests were becoming more heterogeneous.

When dealing with fossil forms, especially compression fossils, it is often not possible to determine if the antennae are geniculate or not and the scape/funicle ratio provides a good indication of this character. While preliminary observations indicate that the majority of weevils with geniculate antennae have a scape/funicle ratio over 0.50, there are exceptions. Some orthocerus brentids have elongate first antennal segments and some gonatocerus tanymecines possess short scapes.

Mesophyletis possesses characters typical of members of the Caridae, Apionidae, and Nanophyidae (Thompson 1992). With the Caridae, the fossil shares a fairly dense elytral vestiture, masked elytral striae, a loose antennal club, a 7-segmented funicle, antennae inserted on the side of the rostrum, approximate eyes, tarsi with divaricate claws, emarginate first tarsal segment, leveled and subequally long abdominal ventrites, and a serrulate outer edge of the meso- and metatibiae. Characters that *Mesophyletis* shares with the Apionidae and Nanophyidae are listed in Table 1.

It is difficult to place *Mesophyletis* in the Apionidae, in spite of its 7-jointed funicle and bifid claws, because that group typically has straight antennae

Table 1. A comparison of characters of Apionidae, Nanophyidae, and *Mesophyletis* (characters for Apionidae and Nanophyidae taken from Zimmerman 1993).

| Character | Apionidae | Nanophyidae | <i>Mesophyletis</i> |
|-----------------------|----------------------------------|------------------------|--------------------------|
| Elongated trochanters | present | present | present |
| Antennal structure | straight | geniculate | geniculate |
| Antennal funiculus | (6)–7 jointed | 4–6 jointed | 7- jointed |
| Antennal club | mostly fused | mostly loosely jointed | loosely jointed |
| Antennal insertions | underside or beneath rostrum | side of rostrum | side of rostrum |
| Antennal scrobes | concealed from side view | exposed in side view | exposed in side view |
| Eye position | well separated | approximate | approximate |
| Scutellum | exposed | concealed | concealed |
| Tarsal claws | often toothed, never connate | never toothed | toothed, divergent |
| Mesocoxal cavities | coalesced or closely approximate | well separated | closely approximate |
| Abdominal ventrites | normal, straight sutures | unequal, sides curved | normal, straight sutures |

with a fused antennal club and a visible scutellum. However, as pointed out by Wanat (2001), some basal apionids (*Lepanomus* Balfour-Browne) have a loose antennal club. The fossil does not fit with the Nanophyidae, even though it possesses geniculate antennae, a loosely 3-segmented antennal club and closely approximated eyes, because nanophyids have antennal funicles composed of only 4–6 segments, the mesocoxal cavities are well separated, the tarsal claws are never toothed, and the ventrites are unequal and curved at the sides.

The bilobed tarsi suggest that *Mesophyletis* was an arboreal species (Blatchley and Leng 1916) and the protective color pattern on the elytra indicates that it was exposed during periods of activity. The long rostrum implies that it fed and possibly oviposited within plant tissues, such as stems, developing flowers, and seeds. The saw-tooth-like serrulations on the metatibia could have supported it while feeding or making ovipositional cavities. The pedunculate lobes on the third tarsal segments and the extended terminal tarsal segments possibly were modifications for grasping smooth surfaces, such as angiosperm leaves or glabrous seed pods.

An early angiosperm host for *Mesophyletis* is possible since members of the Apionidae and Nanophyidae develop predominately in vegetative tissues, galls, fruits, and seeds of angiosperms (Zimmerman 1993). In fact, nanophyids and other seed beetles are important predators of dipterocarp seeds in southeastern Asia, at times destroying between 60 and 100% of the seed crop (Lyal and Curran 2003). It is interesting that the fossil originates from an area where dipterocarps are dominant in forests with an annual rainfall of around 100 inches (Stamp 1925). However, a gymnosperm host cannot be ruled out since some present day representatives of the Apionidae develop on conifers. The North American *Podapion gallicola* Riley develops in galls on pines (Blatchley and Leng 1916) and all species of the endemic Australian genus *Rhinorhynchidius* Voss develop in galls on the leaves and stems of members of the genus *Callitris* in the Cupressaceae (Zimmerman 1994b).

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